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Tamias townsendii.

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Tamias townsendii Bachman, 1839

Townsend's Chipmunk

Tamias townsendii Bachman, 1839:68. Type locality "lower Columbia River, near lower mouth of Willamette River about 25 mi below Portland, Oregon."

Tamias hindei (typ. err. for *hindsii*) Gray, 1842:264. Type locality not definitely known, but probably near mouth of the Columbia River (Howell, 1922:182).

Tamias cooperi Baird, 1855:334. Type locality "Klickitat Pass, 4500 ft, Cascade Mts., Skamania Co., Washington" (see Cooper, 1868:531).

CONTEXT AND CONTENT. The small squirrels known as chipmunks are in the Order Rodentia, Family Sciuridae, either Subfamily Sciurinae (Black, 1963) or Marmotinae (Gromov et al., 1965), and Tribe Tamiini. Both body and facial stripes are present. Two genera, *Tamias* and *Eutamias*, have been proposed for Nearctic chipmunks. *Tamias* was propsoed by Illiger (1811:83) for all chipmunks and is now the genus of all eastern North American representatives. Troussart (1897:220–252) recommended subgenus *Eutamias* for western forms, distinguished from subgenus *Tamias* by the presence of two maxillary premolars (Bryant, 1945). Disagreement exists over whether all North American chipmunks should be included in genus *Tamias*, or only the eastern chipmunk as *Tamias* and genus *Eutamias* or *Neotamias* for the western forms. The system used here (Nadler et al., 1977) proposes that all chipmunks are best referred to the genus *Tamias*, with the single Eurasian species in subgenus *Eutamias*, the eastern North American species in subgenus *Tamias*, and the western North American species in the subgenus *Neotamias*. The distinctness of these three groups has also been supported by immunological techniques (Ellis and Maxson, 1979). The genus *Tamias* Bachman (1839) is a junior homonym of *Tamias* Illiger (1811).

Principally on the basis of large size and white or whitish buff tail edging, ten species and one subspecies were recognized as belonging to Townsend's chipmunk group (Howell, 1929; Merriam, 1897). Of these, five species and one subspecies, *Tamias alleni*, *T. dorsalis*, *T. merriami*, *T. quadrimaculatus*, *T. sonomae*, and *T. townsendii sonomae* [now *T. sonomae*], are no longer retained in the group (Hall, 1981). The other five taxa were considered to be subspecies of *T. townsendii* by Hall and Kelson (1959). Subsequently, three of these subspecies were elevated to species status, *T. ochrogenys*, *T. senex*, and *T. siskiyou*, and revised distributions were described for each; subspecies status was retained for *T. t. cooperi* and *T. t. townsendii* (Sutton and Nadler, 1974). *Tamias townsendii* (sensu stricto) contains two subspecies:

T. t. townsendii (Bachman, 1839:68), see above (*hindii* [typ. err. for *hindsii*] Gray is a synonym).

T. t. cooperi Baird, 1855:334, see above.

DIAGNOSIS. Townsend's chipmunks are characterized by large size, creamy white to grayish underparts, ears that are fuscous to fuscous black anteriorly and smoke gray posteriorly; the dorsal dark stripe is fuscous black, extending from crown to rump, and the other dark body stripes are mostly obsolete anteriorly; the light body stripes are narrow and may be nearly obsolete (Fig. 1). The tail is fuscous black above and the border hairs are tipped with gray or whitish gray; when running, the tail is held erect. Large cheek pouches open inside the mouth, anterior to the molars, and extend back to the posterior base of the ears. There are two annual molts, one beginning in May, and the other in August. The fall molt results in the olivaceous phase, with ochraceous-tawny light stripes, fading in the spring to a more tawny body color with dull white stripes tinged with cinnamon (Howell, 1929).

The dental formula of *T. townsendii* is 1/1, 0/0, 2/1, 3/3, total 22. A small, vestigial upper premolar is present, that distinguishes all western North American chipmunks from the eastern North American chipmunks that lack this tooth. This characteristic was considered to be of little generic value by Ellerman (1940) and Bryant (1945), but White (1953*a*) and Hall (1981) maintained it was of generic significance. The upper molar metaloph, the posterior of two main cross ridges, diverges externally from the anterior protoloph (Maser, 1975).

GENERAL CHARACTERS. Howell (1929) described the body color of Townsend's chipmunk as variable, but tail edgings are uniformly smoke gray or pale buff, never deep buff; sides and upper parts vary from tawny, antique brown or umber to tawny olive, sayal brown, orange cinnamon, or clay color; dark dorsal stripes are black or fuscous black, mixed with sayal brown, mikado brown, or russet; the two medial light dorsal stripes vary from grayish white or smoke gray to ochraceous tawny. In some specimens the outer light stripes are obscured by cinnamon, tawny, or olivaceous hair tips. The rump and thighs range from ochraceous tawny to antique brown, with the thighs somewhat paler and more olivaceous. The hind feet are sayal brown to pinkish buff, clouded with fuscous, and the front feet are similar but paler. Top of the tail is fuscous black shaded with grayish white; lower side of the tail is tawny or clay color bordered by fuscous black, and the hairs are tipped with grayish white. The ventral body color is creamy white or grayish white, in some specimens shaded with pale, pinkish buff. The coastal form, *T. t. townsendii*, is darker, brownish or olivaceous, compared to the lighter, reddish or somewhat orange-shaded inland *T. t. cooperi*. The winter pelage color is similar but somewhat darker, with the dorsal light stripes more buffy white.

Average measurements and range (mm) for 10 adult specimens of *T. t. townsendii* from Portland, Oregon were: total length, 249 (235–363); length of tail, 109.6 (96–125); length of hind foot, 35.1 (34–36); height of ear from notch, 16.1 (15–17.5); greatest length of skull, 38.7 (38–39.5); zygomatic breadth, 21.6 (21.2–21.9); cranial breadth, 16.5 (16.2–17); interorbital breadth, 8.6 (8–9); length of nasal bones, 12.2 (11.6–12.6; Fig. 2). For comparison, average measurements for 10 adult *T. t. cooperi* from the Cascade Mountains of southern Washington were: total length, 250.3 (238–263); tail length, 112.2 (102–120); length of hind foot, 35.7 (34–38); height of ear from notch, 16.8 (15–18); greatest length of skull, 37.9 (36.8–38.7); zygomatic breadth, 21.3 (20.6–22); cranial breadth, 16.2 (15.7–16.5); interorbital breadth, 8.3 (8–8.7); length of nasal bones, 11.9 (11.4–12.4). The head-body measurements are slightly larger for *T. t. cooperi*, but all cranial measurements are slightly larger for *T. t. townsendii* (Howell, 1929).

In a study of sexual size dimorphism in chipmunks, Levenson (1990) found the mean head-body length ($\pm SE$) of 9 female *T. t.*

FIG. 1. A female *Tamias t. townsendii* from 29 k east of Port Orford, Curry County, Oregon.

FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Tamias t. townsendii*. Greatest length of skull 39.8 mm.

cooperi to be 145.11 ± 10.61 mm and 8 males to be 139.63 ± 9.72 mm, and, for *T. t. townsendii*, 143.5 ± 5.31 mm for 20 females and 136.4 ± 8.56 mm for 5 males, also confirming that *T. t. cooperi* is larger in head-body measurements, but *T. t. townsendii* is larger in all cranial measurements. Females were significantly larger than males, and they were larger in areas with severe climate as compared to those living where the climate is more moderate. He found the opposite size-climate relationship for males.

In contrast, Johnson (1943) found subspecies of *E. townsendii* progressively paler in color and of smaller size inland where the climate is more severe. Sutton and Nadler (1974) also found that both sexes of Townsend's chipmunks were larger, and much darker in color, along the Pacific coast where the altitude is lowest and the climate more mild, in contrast to the same species in the high, colder climate of the Sierra Nevada and Cascade Mountains.

DISTRIBUTION AND FOSSIL RECORD. Townsend's chipmunk (*T. t. townsendii*) is found from the Rogue River in southwest Oregon northward along the Pacific Ocean and Coast Ranges to southwest British Columbia, southward in the western Cascade Mountains to the headwaters of the Rogue River about 27 km west of Crater Lake, Klamath County, Oregon (Fig. 3). In southern Oregon, Cooper's chipmunk (*T. t. cooperi*) occurs from northern Jackson and Josephine Counties, in the area between the distributions of *T. t. townsendii* and *T. siskiyou*, northward in the Cascade Mountains to near Hope, British Columbia (Hall, 1981; Sutton and Nadler, 1974). Howell (1929) reported finding many specimens intermediate between *T. t. townsendii* and *T. t. cooperi*

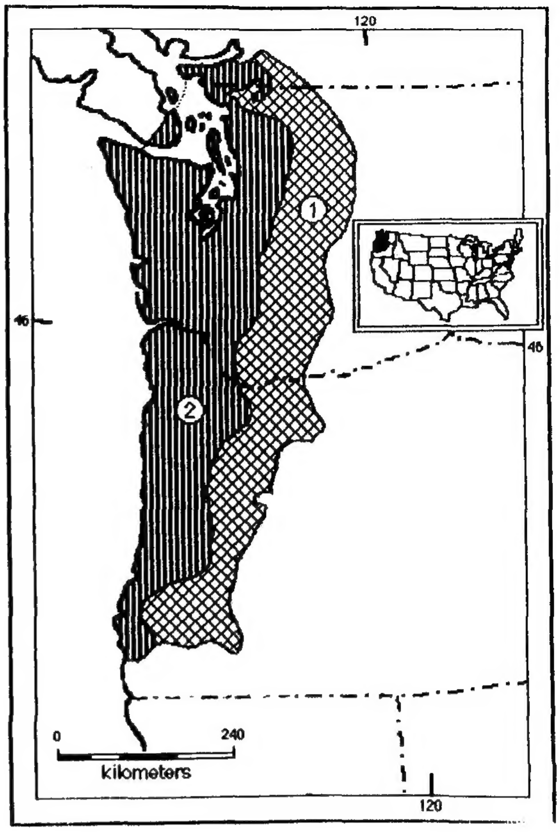

FIG. 3. Distribution of *Tamias townsendii* in the states of Washington and Oregon (Hall, 1981): 1, *T. townsendii cooperi*; 2, *T. t. townsendii*.

along the western base of the Cascade Mountains from near Hope, British Columbia, to the vicinity of McKenzie Bridge, Oregon, an indication of intergradation between the two subspecies. He noted (p. 111) "A large series in winter pelage from Glendale, Oregon is intermediate between *cooperi* and *townsendii*, but apparently nearer to the former; although the series might be expected to show approach to *siskiyou*, which occurs on the slopes of the Siskiyou Range less than 30 miles southwest of Glendale, such is not the case, and apparently the two races do not intergrade at this point." This lends support to classification of *T. siskiyou* as a separate species (Sutton and Nadler, 1974).

Although fossils of the Sciuridae have been found to be almost cosmpolitan in distribution, little is known of the patterns of dispersal and evolution (Black, 1972). Members of the squirrel family first appear in Oligocene time in North America, and by Miocene the chipmunk subgenus *Neotamias* is known from fragmentary, sparse material in the Barstow deposit. Fossils of Townsend's chipmunk have not been recognized in any Pleistocene fauna.

FORM AND FUNCTION. The genital bones are the most reliable diagnostic characters by which to distinguish Townsend's chipmunks, as well as the species of all western chipmunks (Sutton and Nadler, 1974). Intermediate and/or indeterminant specimens were not found, and a positive correlation with body and cranial measurements supports the validity of using these bones as distinguishing taxonomic traits. Both male and female genital bones of *T. t. cooperi* and *T. t. townsendii* are alike and do not differentiate these subspecies, but they are clearly different from those of other species. Although the genital bones of chipmunks are morphologically distinctive for each taxon, the genetic control of their structure is unknown, and it is conceivable that intermediates may not exist at zones of potential intergradation. The coefficient of variability of baculum shaft measurements was found by White (1953*b*) to be only 3.85.

Approximate greatest lengths (base to distal end of tip) of bacula of both *T. t. cooperi* and *T. t. townsendii* were 2.9–3.3 mm (Hall, 1981; Sutton and Nadler, 1974). Greatest length of the baubella

for both subspecies was 1.2 mm (Sutton, 1982). Usefulness of the genital bones as diagnostic traits separating the taxa of western chipmunks is shown in the taxonomic key in Hall (1981:340–342).

Mammae of the females are arranged in 4 pairs, 1 inguinal well back, 2 abdominal, and 1 pectoral, about evenly spaced on the 2 long mammary glands extending the length of the belly (Bailey, 1936).

ONTOGENY AND REPRODUCTION. Strong environmental seasonality is responsible for determining timing and intensity of reproduction in *T. t. cooperi* living in the temperate montane regions of the eastern Cascade Mountains of Washington (Kenagy and Barnes, 1988). After 4–5 months of hibernation or intermittent activity, reproduction is concentrated in late spring and summer when climate and food availability are most satisfactory, and when the warm season allows the young to mature sufficiently to make preparations and hibernate in the fall. Apparently each individual prepares its own food store for the winter. Soon after emerging from hibernation, breeding was observed during the last week of April and lasted about 2 weeks. Gestation was estimated to be 28 days, and parturition occurred in late May and early June. The first young emerged from the nest in early July, and the latest lactation was in early August. Some males remained sexually active after the 2 week breeding period. One chipmunk was observed with enlarged testes (480 mg) on 20 June; enlarged seminal vesicles (101 mg), and substantial spermatozoa were present. In July, another male had enlarged testes (369 mg) and seminal vesicles (112 mg), but no sperm. Judging from the collection records, there was no successful late season mating by these individuals. Of the adult males, 30% examined between 7 April and 20 June, had unenlarged testes and were judged to be nonbreeding. Nearly all of these were yearlings (14 of 15); however, 20% of the reproductively active males also were yearlings. Detection of nonbreeding in *T. t. cooperi* was difficult, but data suggest that as many as 33% of the females may not have bred. Resorption of 9% ($n = 11$) of the embryos following fertilization represented a downward adjustment of litter size, perhaps in response to environmental conditions. At the time of emergence from the den the average-sized litter had nearly twice the body mass of the mother (170%), with mean litter size of 3.8 young. This was a much smaller mean litter size than that of 6.1 for *T. senex* (Tevis, 1955).

Two gravid female *T. t. cooperi* were captured 52 km east of Sweet Home, Linn Co., Oregon and the development of their offspring was reported until they achieved sexual maturity and breeding was initiated in the spring of their second year (Forbes and Turner, 1972). One female gave birth to 5 young on the night of June 17–18; the other gave birth to 4 young on the night of June 23–24. Average mass of the litter of 4 at birth was 3.8 g (3.5–3.9); mean total length was 57.5 mm (56–58); mean length of tail vertebrae was 14.8 mm (14–15), and mean length of hind foot was 7 mm. The ears were folded and could not be measured. At 10 days the body mass was 9.4 g (9–10), total length was 89 mm (87–91), length of tail vertebrae was 27.5 mm (26–28), length of hind foot was 12.6 mm (12–13), and length of ear was 4 mm (4). At 20 days body mass was 19.2 g (18.1–20.4), total length was 129.2 mm (128–130), length of tail vertebrae was 49.7 mm (49–50), length of hind foot was 22.0 mm (22), and length of ear was 8 mm (8). At 34 days of age the average body mass was 33.7 g (33.0–34.8), total length was 189.2 mm (187–192), length of tail vertebrae was 90.0 mm (88–91), length of hind foot was 32.5 mm (32–33), and length of ear was 14 mm (14). At birth the translucent skin was loose, pink, and bare except for vibrissae; toes were webbed and ended in tiny, white claws; subdermal fat deposits were visible; external genitalia were not discernible; oral openings were small and the lower lips were covered with tiny, unpigmented hairs; epithelium had begun to slough off and continued to be lost to the 9th day; eyelids were fused, with no visible cleft; pigment of the eyeballs could be seen through the skin, and pinnae of the ears were about 13-mm long, folded downward to cover the external auditory meatus. At 10 days dorsal hair growth had extended onto the proximal portion of the tail, shoulders, and flanks, and the adult pattern of head and body stripes was apparent. Some fat deposits were still visible under the skin, plantar tubercles were present, and the claws were dark at the bases and white at their tips, with tips of lateralmost toes beginning to separate; eyelids were still closed, but the cleft was visible between the lids; the external auditory meatus was still closed. The pups no longer gyrated helplessly but remained venter down and moved by pulling or pushing with the forelimbs, while the hind limbs took no part in locomotion. By 20 days of age the fur was sleek and long enough to stand partially erect; the lower incisors had appeared; the toes were separated, and the hind limbs occasionally provided spasmodic thrusts. Females were more irritable than males, and the pups were strong and active. At day 22 the first tail-waving was noticed, and at 24 days the external auditory meatus opened and the hind legs were more coordinated. The eyes opened and the upper incisors erupted between days 27 and 29. By the fifth week the coats were bright and fuzzy, with markings even more distinct than on the coats of adults. They began to eat rolled oats and drink from the water bottle, and appeared to adjust easily when the mother was removed from the cage. By day 40 the upper deciduous third and fourth premolars were visible above the gum tissue. By 90 days all molars and the permanent upper fourth premolars were at or near occlusal level. At about 3 months of age the pups were judged to be adults, as determined by dentition. Breeding was not initiated until the spring of their second year of life.

ECOLOGY. Periods of greatest daily activity of *T. townsendii* occurred in late morning and early afternoon (Trombulak, 1985). In a study plot of 6.24 ha the mean home range from April through June was 0.80 ha with 2.6 adults/ha. Foods included seeds of grasses and pines, and the fruits of huckleberry (*Vaccinium* sp.), bride's bonnet (*Clintonia uniflora*), wild strawberry (*Frageria virginiana*), bearberry (*Arctostaphylos uvi-ursi*), bunchberry (*Cornus canadensis*), wild rose (*Rosa spaldingii*), fungi, and one animal ate tree bark. In eastern Washington *T. townsendii* and *T. amoenus* overlap in habitat use, diet, and time of daily activity. The home range for each was influenced by body size, trophic category, population density, competition, habitat complexity, food density and distribution, and habitat productivity. Size of the original home ranges of the two species was the same on both experimental and control grids. Both species used areas with the same vegetation density and percent of canopy cover, and, although the overlap was lowest for the use of space, the interspecific interactions apparently did not result in differential use of microhabitats. Observed diets overlapped broadly in the use of grass seeds, pine nuts, and the fruits of several understory plant species. *T. amoenus* favored seeds while *T. townsendii* favored the fruits. Both species were highly aggressive, with interactions of lunge, bite, or chase, never coming within sight of each other without eliciting an aggressive response. When *T. townsendii* was removed, size of home range for *T. amoenus* increased, either the result of actual increase in home range size or through the recruitment of additional *T. amoenus* individuals into the experimental grid area. The presence of *T. townsendii* inhibited the recruitment of juvenile *T. amoenus* to an area. Interspecific competition should be considered when interpreting home range.

A different sympatric relationship was found in Mount Rainier National Park, Washington, at an altitude of 1,830 m where the home ranges of *T. t. cooperi* and *T. amoenus ludibundus* overlapped extensively (Meredith, 1972). Both species used tree islands of this subalpine area extensively, perhaps because of the high cover, which provided safe avenues of travel to foraging areas. The tree islands were dominated by subalpine fir and mountain hemlock, with intervening heather patches, and ecotones. Only small numbers of both species were collected in areas covered by lupine, or in those areas in which black alpine sedge predominated. Townsend's chipmunks used the talus areas much more than did the yellow pine chipmunks. It is conceivable that the patchy habitat model helped make it possible for the two species to coexist. Only in early spring when snow was still on the ground would food have been a limiting factor to their distribution. Burrow site availability may have limited home ranges for females, since in one grid, home ranges of female *T. amoenus* were not found near the home ranges of female *T. townsendii*. Overlap of home ranges of female *T. townsendii* was minimal, suggesting exclusive range use by each individual. Females of *T. amoenus* were excluded from the talus areas used by *T. townsendii* females for their burrows.

Riparian and upland habitats differ in abundance of small mammals, number of breeding adults, number of juveniles, mass of adult males, and patterns of microhabitat selection (Doyle, 1990). *T. t. townsendii* was captured most often in the upland habitats where the predominant herbs were twinflower (*Linnaea borealis*), bracken fern (*Pteridium aquilinum*), starry solomon plume (*Smilacina* sp.), and moss ground cover. The common evergreen shrubs and trees were salal (*Gaultheria shallon*), Pacific rhododendron

(*Rhododendron macrophyllum*), trailing blackberry (*Rubus* sp.), Oregon grape (*Berberis nervosa*), Douglas fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*). In the upland areas the maximum air temperature and absolute range of air temperature were consistently higher than in the riparian grids. In the riparian habitat area the evergreen herbs, Oregon oxalis (*Oxalis oregana*), western swordfern (*Polystichum munitum*) and starry solomon plume (*Smilacina stellata*) were present, along with the shrubs, trailing blackberry (*Rubus* sp.), red huckleberry (*Vaccinium parvifolium*), and California hazel (*Corylus cornuta*); trees were big-leaf maple (*Acer macrophyllum*), vine maple (*Acer circinatum*), and red alder (*Alnus oregona*), along with the Douglas fir and western hemlock that were in the upland area. In the riparian habitats a larger proportion of *T. townsendii* adult males and a significantly greater proportion of adult females were in breeding condition. More juveniles were present in the upland habitats. Riparian habitats tend to act as a species source while upland areas act as a dispersal sink. The abundance of chipmunks was correlated with the presence of decayed logs, everygreen herbs, shrubs and trees, few deciduous herbs and trees, and a high percent of lichen cover.

In a habitat preference study, *T. townsendii* was collected almost exclusively in clearcut areas from which all the trees had been removed. In July their food consisted of 27% fungi and lichens, 37% conifer seeds, and 35% other material, mostly pollen, but included some shrubs, herbs, and seeds. In an area that was clearcut and the slash burned, the food was 68% fungi and lichens, 18% conifer seeds, 2% shrub, herb and seed material, and 12% invertebrates. It appeared that the chipmunks increased in numbers following clearcut logging because herbaceous and shrubby vegetation became much more abundant (Horn and Babb, 1983).

The typical habitat of *T. townsendii* is composed of mesic, closed-canopy forest and dense brushy thickets. As expert climbers, these chipmunks have relatively larger brains than three other species of less arboreal chipmunks in Oregon (Budeau and Verts, 1986).

Townsend's chipmunks use a wide range of foods, including nuts, seeds, berries, and other fruits, roots, bulbs, green vegetation, insects, and small animals (Bailey, 1936). At Multnomah Falls, Oregon chipmunks feed on salmonberries (*Rubus spectabilis*), red and black elderberries (*Sambucus* sp.), gooseberries (*Ribes* sp.), crab apples (*Pyrus rivularis*), plums (*Prunus* sp.), and the seeds of maple (*Acer* sp.), boxelder (*Acer negundo*), dogwood (*Cornus* sp.), buckeye (*Aesculus californica*), pine (*Pinus* sp.), rose (*Rosa* sp.), thistles (*Cirsium* sp.), grasses, and grains. Many species of mushrooms, bulbs, and the tubers of fireweed (*Epilobium angustifolium*) are eaten. Hazelnuts, acorns, and hemlock seeds are sought after for winter stores. Individuals were collected with 5 acorns, 19 sugarpine seeds, or 65 unidentified pine seeds in a cheekpouch load.

The mature fruiting bodies of underground fungi (truffles), which emit a strong odor when mature, were a preferred food of *T. townsendii*. Spores of *Rhizopogon* and *Melanogaster* were especially common in the feces, and it appeared that these animals were primarily mycophagous (McIntire and Carey, 1989).

Lodgepole pine, *Pinus contorta*, and white spruce, *Picea glauca*, seeds contaminated with a fungus, *Caloscypha fulgens*, were readily eaten by *T. t. townsendii* on southern Vancouver Island. This fungus, which is pathogenic to the seeds of several conifers, is common in the forest duff in areas where there are infected trees, and was also present in seeds cached by chipmunks. Since presence of the fungus prevents both germination and seed rotting it may be a significant agent in preserving the seeds, and may help to ensure the animals a food supply between cone crops. Also, since the fungus is most prevalent in seedlot trees planted from cache-collected cones, it appears likely that the chipmunks, as well as other rodents, may be significant agents in the dissemination of this harmful fungus. Fecal transmission of the fungus ascospores may also be involved, but the evidence was not conclusive (Sullivan et al., 1984).

Gashwiler (1959) studied *T. t. cooperi* on grids (91 m) set up as control, a virgin forest, one year post logging, and an area that was logged and then slash-burned. Chipmunk populations varied from 0.6 to 1.1 animals/ha in the virgin forest. The population dropped to 0.5/ha in the first year after logging and burning. Burning caused chipmunks to leave the cut area for the timber. During the first year after the burn, they ranged from the timber onto the cut and slash-burned area, but they did not reside where the timber and brush had been completely removed. Logging reduced the number of chipmunks, but the reduction wsa far less than that caused by logging and burning. Prior to the slash burn, 50% of the chipmunks were trapped around the experimental plot; after the burning, 80% were captured around the plot, with travel distances ranging from 123 to 400 m. A year later, from 33.3 to 66.7% of the chipmunks were captured in the same area. These data suggest that chipmunk populations can travel relatively long distances in a short time, and that burning caused chipmunks to leave the logged area for the forest. The population must increase rapidly, however, since Tevis (1956) indicated that cutover areas 3–10 years old had from 2–4 times as many Townsend's chipmunks as a virgin forest.

In a population study of *T. t. townsendii* in southwestern British Columbia from the autumn of 1976 to the spring of 1978, an experimental population was fed sunflower seeds and whole oats as supplementary foods spread weekly around each trap station (Sullivan et al., 1983). The population that was fed increased 40–50% more than the control population, had juvenile survival from four to six times higher, and animals that grew significantly faster. When feeding was withdrawn, population density declined, and related demographic variables became similar to those in the control area. It was concluded that the availability of food limits populations of this chipmunk.

In a trap/release population study of the area around the Trojan Nuclear Power Station in western Oregon, *T. t. townsendii* was collected only in surrounding forests, never in a meadow. In August, 3 of 11 chipmunks showed evidence of bot fly (*Cuterebra* sp.) infestation; in September only 1 of 13 animals was infested (Hedlund and Rickard, 1990). In a study of Coccidians, Hill and Duszynski (1986) found three of four *T. townsendii* examined in Washington to be infected with *Eimeria dorsalis* and *E. cochisensis*.

Since Townsend's chipmunks are common in timber and thickets and along edges of fields of grain and fruits, they may have an economic impact on these products; however, presence of an abundance of wild, natural foods prevents serious injury to domestic products. Consumption of tree seeds may have some influence on the welfare of forests, retarding some reforestation that might otherwise occur. On the other hand, as chipmunks bury and store seeds which may be forgotten, these could grow and be of some value in recovery and reestablishment of a forest (Bailey, 1936).

BEHAVIOR. Activity periods during the warmer months involve feeding and gathering seeds of grasses, herbs, and conifers for storage in a den (Howell, 1929). During the weeks of late summer and fall quantities of food are accumulated for the winter. Hibernation varies among the chipmunks. Those that live in areas where snow is present all winter hibernate during the colder months, but in warmer areas and especially in some places along the Pacific coast, they appear to be active all winter.

The ecological distribution of species in the genus *Eutamias* suggests adaptive differences with respect to periods of activity and torpidity (Cade, 1963). Evidence from the field and from captive studies indicates that these animals do not necessarily enter a state of deep hibernation during the winter, although they may be inactive above ground and lethargic in behavior, with slightly depressed body temperatures for weeks at a time. Such shallow hibernation is an adaptive compromise between the minimum energy requirements of a deep hibernator and the high energy expenditure of a rodent that remains active during the winter. Energy is saved without losing advantages of wakefulness.

Winter dormancy of *T. townsendii* is similar to that of *T. amoenus* in which the animals are intermittent, or in areas with mild climate, even non-hibernators (Stebbins and Orich, 1977). An individual may even lose mass before entering the winter den, so it survives mostly on stored food, and energy is conserved by entering various depths of torpor and by decreased activity.

During a study of the home range of *T. t. cooperi* in Lane Co., Oregon, a juvenile male was first captured in August 1955, and after being trapped 58 more times, was last captured in May 1962 when about 7 years old. His testes were descended and he appeared in good health, with the original tag still firmly attached. Home range for this animal was estimated to be 0.7 ha (Gashwiler, 1965).

Those individuals of Townsend's chipmunks that live in the coastal forest areas, [*T. t. townsendii*] "are quiet and gentle in actions, keeping much in the shadows and under the bushes out of sight. Often they would pass unnoticed but for their birdlike voices. . . . Though the nervous scurry characteristic of the smaller species is lacking, they are quick when escape is necessary—expert climbers and skillful at hiding in trees, bushes, hollow logs, or holes in the

ground. Their homes are in underground burrows, where warm nests and ample stores of nuts and seeds afford all the comforts of chipmunk life. . . . Like most of the squirrel family they are daylight workers, beginning activities with the first clear dawn, and retiring to their nests for the night with the twilight shadows" (Bailey, 1936: 127).

GENETICS. While all chipmunks have a common chromosome number (2n = 38), there are three distinctive karyotypes in North America and a fourth in the Eurasian chipmunk. Two karyotypes (A and B) characterize all western forms, and another pattern, with at least nine chromosomal rearrangements, is found in *T. striatus* of the eastern states. No intrapopulational polymorphism or chromosomal hybrids were found. The karyotype B of *T. townsendii* resembles that of representatives from the eastern foothills of the Rocky Mountains, the adjacent plains, and in widely separated areas on the east and west sides of the Great Basin. This karyotype B group contains all western chipmunks except the species *cinereicollis* and seven subspecies of *T. minimus* (Nadler et al., 1977; Sutton and Nadler, 1969).

The type B karyogram of *T. townsendii* has five groups of chromosomes. Group I contains four similar pairs of large metacentric chromosomes with nearly median centromeres; Giemsa-band patterns are indistinguishable from that of other type B *Neotamias* species. Group II has six pairs of large chromosomes with submedian centromeres, plus one X sex chromosome in the male or two in the female. Group III has four pairs of large acrocentric chromosomes with terminal or nearly terminal centromeres. Group IV has one pair of the smallest metacentric chromosomes, with no Giemsa-bands. Group V is made up of three pairs of small chromosomes of uniform size, with terminal or subterminal centromeres, plus the small Y chromosome of the male, which has no Giemsa-bands. The major difference between this pattern and that of karyogram type A consists of three pairs of small acrocentrics in group V of karyotype B, compared to four pairs in type A. In group I there are four pairs of metacentric chromosomes in karyotype B, compared to three pairs in karyotype A, a difference best explained as a single pericentric inversion. Karyotype B of *T. townsendii* resembles that of representatives from the eastern foothills of the Rocky Mountains, the adjacent plains, and chipmunks from widely separated areas on the east and west sides of the Great Basin (Nadler et al., 1977; Sutton and Nadler, 1969).

Howell (1929) proposed five groups of western chipmunks, based upon morphology and pelage characters. He placed *T. townsendii* in a group along with the presently recognized species: *ochrogenys, siskiyou, senex, sonomae, quadrimaculatus, merriami,* and *dorsalis.* White (1953*b*) proposed three groups, based upon baculum characteristics as well as the structure and appearance of the skull and skin. He placed *T. townsendii* in a group with the species *alpinus, minimus, sonomae, amoenus, dorsalis,* and *merriami,* mostly on the basis of relatively long, slender bacula. Neither of these patterns for grouping the western chipmunks is in agreement with the two karyotype groups (A and B) described by Sutton and Nadler (1969), with *T. townsendii* in group B which contains all western chipmunks except the species *cinereicollis* and seven subspecies of *T. minimus.* There is at present no satisfactory explanation for the existence of two western chipmunk karyotypes since it is unlikely that stasipatric speciation would have occurred in such widely scattered localities.

REMARKS. Statistical analysis of *T. t. ochrogenys, T. t. senex,* and *T. t. siskiyou* showed small but significant differences in external and cranial measurements, and major differences in morphology of genital bones. This provided bases for the three subspecies in California to be elevated to species status as *T. ochrogenys, T. senex,* and *T. siskiyou* (Sutton and Nadler, 1974). To further test the desirability of changing these subspecies to species status, Sutton (1987) analyzed *T. t. townsendii* ($n = 40$), *T. siskiyou* ($n = 131$), *T. senex* ($n = 71$), and *T. ochrogenys* ($n = 54$), all from an area about 32 km wide along the Pacific coast from about 20 km north of the Rogue River, Josephine Co., in southwestern Oregon to Bodega, Sonoma Co., California. These four taxa are so similar in appearance and measurements that the three found south of the Rogue River were all considered to be *E. t. ochrogenys* (Hall and Kelson, 1959; Howell, 1929; Johnson, 1943). However, discriminant function analysis showed obvious differences, and designated river boundaries separated them with no discernible intergradation. The Rogue River separates *T. t. townsendii* on the north and *T. siskiyou* on the south for about 250 km eastward from the Pacific coast; the Klamath River separates *T. siskiyou* from *T. senex,* for a distance of about 240 km eastward from the ocean, and the Eel River is a boundary between *T. senex* and *T. ochrogenys* near the Pacific. It appears reasonable that large rivers should serve as barriers to chipmunk disribution, but the Rogue River, as well as those of northern California are all small, especially in late summer and fall.

Based upon geographical variation in cranial and mandibular morphology and external body measurements, as well as cladistic analysis of electrophoretic data, Levenson and Hoffmann (1984) suggested that there was no basis for the reclassification of the California representatives of the Townsend chipmunk group. They also maintained that inferential conclusions were used by Patterson and Thaeler (1982) in their assertion that direct selective pressures upon the baculum result in little bacular variation. They do not agree that the baculum functions to bring about reproductive isolation. There is reason, therefore, to further investigate the taxonomic status of Townsend's chipmunks, and the use of genital bones as major characters used in the classification of all western chipmunks should be reevaluated.

The genus name *Tamias* means "steward," an appropriate reference to the management of seeds stored for food by chipmunks (Jaeger, 1955).

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